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REVIEW

Performance of melon hybrids derived from parents of diverse geographic Origins

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Abstract Genetic relatedness and phenotype are important factors that govern the expression of heterosis in hybrid progeny of many cross-pollinating plant species. Since this relationship is important but not well understood in melon (*Cucumis melo* L.), one monoecious and two andromonoecious melon lines of diverse Chinese [Peoples Republic of China (PRC)] origin were crossed to the andromonoecious U.S. Western Shipping market type 'Top Mark' (TM) and the andromonoecious, highly branched line H-16 to determine parental combining ability and heterosis for five yield component traits in three test environments [open-field (USA), and energy-saving (PRC) and plastic greenhouses (PRC)]. Random amplified polymorphic DNA (RAPD)- and simple sequence repeat (SSR)-based genetic distances (GD) among and between parents (5) and their hybrids (6) were calculated and compared to phenotypic trait values. These germplasms were evaluated for lateral branch number (LBN), days to 50% flower (DF), fruit number and weight per plant, and fruit length:diameter (L:D) ratio in each of three test environments. General combining ability was significant for all characters, except for L:D in all locations, and LBN and DF in the plastic greenhouse environment. Both descriptors of difference (genetic marker and phenotype) were discriminatory, and provided similar assessments of relationships among parents and hybrids. Although dramatic performance differences were detected between parents and among F_1 hybrid progeny, a strong relationship between GD and heterotic effects was not consistently detected.

Keywords Heterosis · Germplasm · Combining ability · Yield · Yield components

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Introduction

Melon (*Cucumis melo* L.; 2n = 2x = 24) is an important horticultural crop worldwide, where the introgression of unadapted germplasm continues to be critical to plant breeding efforts. Considerable morphological variation exits in vegetative (i.e., plant architecture) and fruit characteristics (e.g., size, shape, color and texture, taste, and composition) making melon one of the most phenotypically diverse *Cucumis* species (Kirkbride 1993; Whitaker and Davis 1962). Wild forms (e.g., ssp. *agrestis*) and landraces of C. *melo* can be found in the Middle East and Asian (Staub et al. 1987) that are cross-compatible, but genetically distant from commercial melon (Mliki et al. 2001; Staub et al. 2004). However, such genotypes have been historically important in plant breeding.

Commercial melons are divided into seven distinct botanical groups including: (1) *C. melo agrestis* Naud (wild melon); (2) *C. melon flexuosus* Naud (snake melon); (3) *C. melon conomon* Mak. (pickling melon, Chinese white cucumber); (4) *C. melon cantalupensis* Naud. (cantaloup or muslmelon); (5) *C. melon indodorus* Naud. (winter melons, honeydew, Casaba); (6) *C. melon chito* (mango melon) and dudaim Naud. (Queen's pocket melon), and; (7) *C. melon momordica* (Phoot or Snap melon). (Munger and Robinson 1991). Due to its fruit characteristics, Chinese melon (not delineated to a common market class, but phenotypically similar to Groups Inodorus, Monordica, and Conomon in some exterior fruit characteristics; Luan et al. 2008) differs dramatically (i.e., pathogen susceptibility, and fruit taste and texture) from other major market class melons (e.g., U.S. and European Shipping, Ogen, Galia, and Charentais), and thus is an important component of the primary gene pool for plant breeding.

Genotype × environment (G×E) interactions may be important considerations when genes providing adaptation to one environment are transferred to genotypes adapted to another environment. In fact, the adaptability of a genotype to diverse environments is commonly evaluated by performance in differing different environments (i.e., minimal G×E; Campbell and Jones 2005). Thus, genotypic stability and performance is often directly related to growing environment and G×E.

Phenotypic and molecular variation has been used to characterize relationships among intraspecific and landrace melons (Stepansky et al. 1999; Staub et al. 2004). A myriad of molecular marker types have been used to investigate melon market class diversity (García et al. 1998; Katzir et al. 1996; Monforte et al. 2003; Staub et al. 1997; Silberstein et al. 1999; Stepansky et al. 1999). However, simple sequence repeat (SSR) and random amplified polymorphic DNA (RAPD) markers have proven to be most useful in this regard (Mo Suk et al. 1999; Staub et al. 2000). For instance, García et al. (1998) successfully used RAPD variation to differentiate elite melon germplasm (e.g., Galia vs. Piel de Sapo market classes), where there was a relatively high correspondence between marker loci and some agronomic traits in the germplasm examined ($R^2 = 0.79$).

The tandem use of phenotypic and marker-assisted selection can produce dramatic, economically important changes in breeding populations. For example, heritable marker-trait associations have been used effectively to augment phenotypic selection in cucumber (*C. sativus* L.) (Fazio et al. 2003; Fan et al. 2006). Although potentially useful yield-related marker-trait associations in melon have been identified (Zalapa et al. 2006; Paris et al. 2008; Cuevas et al. 2008), marker-assisted selection (MAS) for plant improvement has not been evaluated in this species.

Combining ability [general (GCA) and specific (SCA)] and heterosis analysis can be used to investigate heterotic response (Singh and Sharma 1989; Cress 1966; Teklewold and Becker 2006). Molecular markers have been utilized to study genetic diversity and its relationship to heterosis in different plant species. Xiao et al. (1996) demonstrated that the close relationship between genetic diversity of hybrids performance and heterosis in rice (*Orzya sativa* L. *iaponica* and *Orzya sativa* L. *indica*). There is general agreement that GCA and associated heterotic effects are important determinates of parental choice during hybrid melon development (Ferreira et al. 2002; Souza et al. 2002). Moreover, heterosis, as a function of performance, is often related to degree of genetic relatedness [i.e., genetic distance (GD)] and is dramatically influenced by growing environment.

Chinese (Groups Indorus and Momordica) and U.S. (Group Cantalupensis) melon market classes

differ dramatically in morphology and relative genetic diversity (Luan et al. 2008). If an association could be found between genetic distance and heterosis in melon, then hybrid analysis (GCA/SCA) of germplasm derived from intercrosses between such market types might be used more effectively to identify heterotic effects during hybrid development. Therefore, a study was designed to: (1) estimate the degree of genetic relatedness between Chinese and US parental germplasm and their derived F_1 progeny were used to estimate heterosis (GCA and SCA), and; (2) evaluate the relationship between GD and heterosis for F_1 hybrid performance prediction.

Materials and methods

Plant materials

Five melon lines (3 Chinese and 2 U.S.) were used to create non-reciprocal hybrids where Chinese and U.S. lines were used as maternal and paternal parents, respectively (Table 1). Chinese germplasm was originally acquired from farmers (Qinggang, Heilongjiang Province) by Heilongjiang Aolong Agriculture Limited Company (HLJAL), Harbin, Heilongjiang Province, PRC in 1998, and then inbred by self-pollination to produce lines ($>S_4$) that were subsequently used to create F_1 hybrids (5) between these and U.S. lines originating from the U.S. Department of Agriculture (USDA) melon breeding project in Madison, Wisconsin.

All multiple disease resistant Chinese lines employed herein possess early concentrated flowering ($\sim$15 days from transplanting) and high yield (2–4 fruits/plant/harvest) under typical open-field northern Chinese growing conditions (i.e., north of the Yanzi River). However, Chinese parental lines differ in sex expression (i.e., line 3-2-2 is monoecious, and 'Yucui' and 'Tianshuai' are both andromonoecious). Chinese female parental lines are early flowering, rapid maturing genotypes that develop multiple lateral primary branches (6–12) bearing many (6–10 fruits/plant) relatively small (100–400 g) fruits near the crown of the plant. 'TopMark' is an andromonoecious U.S. Western Shipping line that possesses between 2 and 4 lateral branches, and produces a diffuse, distal fruiting setting habit typical of most vining melon types. In contrast, the monoecious USDA line H-16 possesses a fractal architectural type (5–8 primary branches), and was derived by selection for increased lateral branches from USDA 846-1 (Zalapa et al. 2006). It has a concentrated fruit-set (2–5 fruits/plant near the crown of the plant), and is capable of multiple fruiting cycles at U.S. commercial spacing (0.35 m within row spacing on 2 m centers; $\sim$14,400 plants/ha).

Morphological evaluation

An evaluation of morphology and comparative productivity (i.e., yield components as defined by Zalapa et al. 2006) of the commercial control ('Tedalongtain No. 1), parents, and their derived F_1 hybrids was carried out in an open-field (OF) in 2005 at the Hancock Agricultural Station, University of Wisconsin, Hancock, Wisc., and in "energy-saving" (ESG; glass, active solar heating) and conventional plastic (PG) greenhouses at the Agricultural Experiment Station, Northeast Agricultural University, Harbin, PRC in 2006. In the U.S., seeds were sown on May 16, and seedlings at the two-leaf stage were "hardened-off" outdoors for 3 days and then transplanted to rows covered with 1 mm black plastic. Plants were spaced 0.30 m within rows on 2 m centers ($\sim$14,400 plants/ha) in Plainfield loamy sand (Typic Udipsamment) soil. Seedlings were transplanted to a randomized complete block design (RCBD) consisting of three replications with 10 plants per plot.

In China, 20 seeds of parental lines and their F_1 hybrids were initially sown in compost vermiculite, and germinated on a heated bench (28–30°C). Seedlings at two-leaf stage were transplanted to ground beds [20–24°C, under fluorescent lights (300 μmol m^2 s^{-1}) providing a 16 h photoperiod] in ESG and PG. The soil type in ESG and PG environments was "Chernozem", consisting of organic matter at 4.6% ($\sim$47 g/kg), where total N, P, and non-exhangeable K was 2.06 g/kg, 0.55 g/kg, and 987.6 mg/kg, respectively. Available N, P, and K was 192.5 mg/kg, 32.4 mg/kg, and 107.7 mg/kg, respectively. Cation exchange capacity (CEC) of the soil media was 25.0 μmol/kg and the PH was $\sim$7.0.

During the spring (March–June) the mean soil temperature in the ESG at 10 cm depth was 20.5°C ranging between 8 and 25°C, while in the PG mean temperature was 19°C ranging between 6 and 27°C.

Table 1 Five melon (*Cucumis melo* L.) lines and their derived F_1 hybrids used for genetic analyses in three growing environments

Origin[a]	Accession or group designation[b]	Cross/parent and sex expression[c]	OP/F_1/ line[d]	Seed source[e]	Market class[f]	Lateral branch number	Days to 50% flowering[g]	Fruit number per plant	Fruit weight (kg)	Fruit length: diameter ratio
China	Tedalongtian No.1 (commercial control)	A	OP	HLJAL	TNK	>10	26	2	0.5	1.3
U.S.	TopMark	M	L	USDA, ARS	TK	2–4	34	2	0.7	1.5
U.S.	H-16	M	L	USDA, ARS	TK	8–10	32	2	0.8	1.5
China	Yucui	A	L	Farmer	TNK	>10	28	3	0.85	1.6
China	Tianshuai	A	L	Farmer	TNK	>10	28	2	0.65	1.5
China	3-2-2	M	L	Farmer	TNK	>10	28	5	0.45	1.25
U.S. × China	Group 1	Tianshuai × TopMark	F_1	–	TK					
U.S. × China	Group 2	Yucui × TopMark	F_1	–	TK					
U.S. × China	Group 3	3-2-2 × H-16	F_1	–	TK					
U.S. × China	Group 4	Tianshuai × H-16	F_1	–	TK					
U.S. × China	Group 5	Yucui × H-16	F_1	–	TK					
U.S. × China	Group 6	3-2-2 × H-16	F_1	–	TK					

[a] U.S. = Madison, Wisc. and China = Heilongjiang Aolong Agricultural Limited Company, Harbin, Heilongjiang Province

[b] Groups defined by cluster analyses (Figs. 1 and 2)

[c] *M* monoecious and *A* andromonoecious

[d] *L* inbred line, *F_1* hybrid, and *OP* open-pollinated variety

[e] *USDA, ARS* U.S. Department of Agriculture, Agricultural Research Service, Madison, Wisc.; *HLJAL* Heilongjiang Aolong Agricultural Limited Company, and *farmer* Grower in Qinggang village in Heilongjiang Province

[f] *TK* thick-skinned and *TNK* thin-skinned

[g] Days from sowing where 50% of the plants in a plot demonstrated at least one fully expanded corolla

In the fall (September–November) the mean soil temperature in the ESG at 10 cm was 20.5°C ranging between 27 and 12°C, while in the PG mean temperature was 22°C, ranging between 10 and 28°C. There are about 90–140 frostless days in Heilongjiang province, where rooting depth ranges between 10 and 25 cm in ESG and PG growing environments.

In ESG and PG, three replications of each treatment containing five plants each were arranged in a RCBD such that plant spacing were spaced 0.30 m within rows on 3 m centers (~12,000 plants/ha). 'Tedalongtian No. 1' seedlings originating from HLJAL were used as transplants for end- and side-borders.

Plants in all experiments were assessed for days to 50% flower (DF), lateral branch number on the main stem (LBN), fruit length (L):diameter (D) ratio (L:D), and fruit number (FN) and weight (FW) per plant (Table 2). Days to anthesis was taken as the number of days from transplanting to the time of ~50% flowering of plants within in a plot. The numbers of primary branches for each plant were counted 30 days after transplant to include all branches of more than 12.5 cm in length below the fourth node. Fruit number and fruit weight (kg) data were collected per plant when fruit were mature (i.e., at the full-slip maturity) over a 25-day harvest period. The average weight per fruit was calculated for each plant by dividing the total number of fruit per plant band by the total weight per plant.

Table 2 Genetic distance (GD) estimates among melon (*Cucumis melo* L.) parental lines as defined by RAPD (Jaccard's GD; lower diagonal) and SSR (Nei's GD; upper diagonal) marker variation

RAPD[a]	SSR[b]				
	TopMark	Line H-16	Yucui	Tianshuai	Line 3-2-2
TopMark	0	0.5	0.53	0.61	0.61
Line H-16	0.12	0	0.74	0.71	0.71
Yucui	0.17	0.27	0	0.45	0.45
Tianshuai	0.29	0.39	0.13	0	0
Line 3-2-2	0.29	0.39	0.13	0	0

[a] Estimated according to Jaccard (1908)

[b] Estimated according to Nei (1973)

DNA extraction

A random sample of 18–20 greenhouse-grown plants (see above) of each entry were harvested at the two- to three-leaf stage, and then bulked for analysis. DNA was extracted from leaf tissue using a CTAB extraction procedure modified according to Luan and Sun (2005). The DNA was quantified on a TD-360 (Turner Designs Instrument, Sunnyvale, Calif., U.S.A), and the final DNA concentration of samples was adjusted to 3 ng/μl with 0.1 M Tris buffer.

PCR amplification

For RAPD analysis, 49, 10-mer primers were purchased either from Operon Technologies (OP; Alameda, Calif.) or the University of British Columbia (BC; Vancouver, BC, Canada). Primers were chosen based on their polymorphic frequency in diverse melon populations, and have successfully been used for genetic diversity analyses as a marker reference array (Staub et al. 2000; Mliki et al. 2001; López-Sesé et al. 2002). The optimized PCR reaction contained 15 ng DNA, 0.3 mM primers, 0.3 mM dNTPs, 4.0 mM $MgCl_2$, commercial Taq DNA polymerase buffer, and one unit of Taq DNA polymerase in a 15-μl final volume. Thermocycling was performed using the following profile: 94°C/4 min; 40 cycles of 94°C/1 min, 36°C/90 s, 72°C/120 s; 72°C/6 min, followed by an indefinite soak at 4°C. After amplification, 5 μl of loading dye was added to each reaction tube. PCR products were electrophoresed according to Horejsi and Staub (1999) in 1.6% agarose gels with 0.5 μg/ml of ethidium bromide in 0.5 × TBE buffer at 180 V and 500 mA using a horizontal-gel electrophoresis system (BRL, Life Technologies, Gaithersburg, Md.) for 3.0 h. Gels were immediately photographed using Gel Expert Software and its associated video imaging system (Nucleo Tech Corporation, San Mateo, Calif.).

For SSR analysis, 21 pairs of microsatellite primers were synthesized as described by Nakata et al. (2005a, b). The optimized PCR reaction contained 15 ng DNA, 0.5 mM primers, 0.5 mM dNTPs, 4.0 mM $MgCl_2$, commercial Taq DNA polymerase buffer, and one unit of Taq DNA polymerase in a 20-μl final volume. Thermocycling conditions were: 96°C/5 min; 40 cycles of 94°C/1 min, 55°C/90 s, 72°C/120 s; 72°C/6 min, followed by an indefinite soak at

4°C. Products were run in 4% agarose gels in 1 × TBE buffer at 5 V/cm and 110 W using horizontal-gel electrophoresis for 3.0 h. Gels were stained and photographed as described above.

Data analysis

A binary data matrix obtained from scoring polymorphic RAPD and SSR bands was used to calculate Jaccard similarity coefficients (Jaccard 1908; RAPD) and Nei's distance-D (Nei 1973, 1978) to define genetic distances (GD) employing computer algorithms in NTSYS (version 2.1) (Rohlf 1997). DNA fragments were scored as present (1) or absent (0) for 27 RAPD and 23 SSR markers. Prior to GD estimation, Jaccard's coefficients were converted by calculating the complement of each coefficient (1-Jij) according to by Spooner and Neieenhuis 1996. Cluster analysis (Sorensen 1948) of GD matrices was used to analyze and graphically depict genetic relationships among accessions using NTSYS 2.1. Jaccard's-based pair-wise GD estimates were then used for comparative analyses employing the unweighted pair-group method average (UPGMA) clustering procedure (NTSYS 2.1).

In as much as the parents used in this study were specifically selected, and parents and locations were of limited number, they were considered fixed effects, and replication and experimental error were considered random effects. Hence, inferences drawn from these data were only applicable to the parents and environments examined. The statistical model used for data analysis within each location was:

$$P_{ijk} = \mu + M_i + F_j + (MF)_{ij} + B_k + \varepsilon_{ijk};$$

where the phenotypic value of the mating of the ith male parent to the jth female parent in the kth replication; μ, the population mean; M_i the effect of the ith male parent; F_j the effect of the jth female parent; $(MF)_{ij}$ the interaction effect associated with the cross of the ith male parent to the jth female parent; B_k the effect of the kth replication, and ε_{ijk} is a residual.

Morphological data were subjected to analyses of variance (ANOVA) followed by least significant difference (LSD) mean comparisons using SAS (SAS Institute 1992). Means, standard deviation, coefficients of variation, and variable ranges were calculated to describe parental and hybrid variation. Analysis of variances were performed using the SAS, and each variance estimated was tested for significance. The model used for treatment analysis was: $Y = \mu + L + R(L) + F + L \times F + R(L) \times F + e$; where Y is the trait, μ is the common effect, L is the location effect, R(L) is the replication within location effect, F is the effect of F_1 families, L × F is the location and F_1 performance interaction, R(L) × F is the replication within location and F_1 families interaction effects, and e is a residual effect. Simple, Spearman Rank correlations (r) were also calculated for the traits examined by location, and then between GD and heterotic and GD and combining ability effects.

Mid-parent (MH), high-parent (HH, synom. over-parent heterosis), and relative high-parent (RHH) heterosis were calculated employing the model:

$$MH = \{[F_1 - 1/2(P_1 + P_2)]/[1/2(P_1 + P_2)]\} \times 100\%;$$

$$HH = (F_1 - P_h)/P_h \times 100\%, \text{ and;}$$

$$RHH = \{[F_1 - (1/2)(P_1 + P_2)]/[(1/2)(P_1 - P_2)]\} \times 100\%;$$

where F_1 is the mean of the hybrid, P_1 the mean of female parent, P_2 the mean of the male parent, and P_h the mean of the best parental performance.

Parental general (GCA) and specific (SCA) combining ability were estimated according to Comstock and Robinson (1948) using the model:

$$X_{ijk} = \mu + g_i + g_j + s_{ij} + r_k + \varepsilon_{ijk},$$

where X_{ijk} the phenotypic value of mating of the ith parent with the jth parent in the kith replication; μ the population mean; g_i GCA effect for the ith parent; g_j GCA effects for the jth parent; s_{ij} SCA effects of the ith and jth parents (according to Griffing 1956); b_k effect of the kth replication, and the ε_{ijk} was the error, and the stand errors of the effects were calculated according to the equations used by Owens et al. (1985).

Results and discussion

Genetic diversity

The 27 RAPD primers used to access genetic diversity among the five melon parents provided 44 polymorphic bands, and 23 SSR primers provided 39

polymorphic bands for examination of parental stocks and cross progeny (data not presented). The average number of banding morphotypes identified herein was similar to a previous study that evaluated highly diverse African melon landraces (Mliki et al. 2001; data not presented). Two of 21 SSR primer products (N29 and N12) were monomorphic across the accessions examined. The number of SSR polymorphic banding morphotypes detected within these accessions ranged between one (primer N29) to eight bands (primer CMGA172), where the size of most of the 39 SSR banding morphotypes was 150 bp or less. Likewise, 27 RAPD primers provided 47 RAPD banding morphotypes (550–2000 bp), where the band number detected among accessions ranged between three (Primer W07) to eight bands (Primer BC252). The variation detected using RAPD primers (~43%) was predictably less than that produced by SSR primers (~84%).

Initial estimates of genetic variation in melon as detected by RAPDs were relatively low (~18%) (Baudracco Arnas and Pitrat 1996). More recent studies, however, have identified higher levels of polymorphism in elite commercial germplasm from a restricted origin (49%) (García et al. 1998). Although the banding morphotypes used herein were fewer than those used by Staub et al. (2000) to examine 46 elite European and U.S. germplasm accessions (49 vs. 135), they did allowed for discrimination among the lines examined.

Variation observed after amplification by primers B12, AD14, AK16, and AT01 RAPD were important in the detection of genetic differences among and between lines (42% of the variation explained; data not presented). While RAPD bands produced by primers C01, D07, I04, W07, AT05, AT15, and AW10 were polymorphic in ≤10% of the parental lines, bands developed using SSR primers CMGA172, CMAT141, and CMCT505 were polymorphic in 57% these lines (data not presented). Since the SSR markers employed were generally more efficient (per primer basis) than RAPD markers in discriminating closely related parental germplasm (e.g., TM vs. line H-16), SSR-based marker arrays will likely be most useful for detection of relatively small genetic differences among closely related melon germplasm.

Genetic relationships among parental accessions and their hybrids based on RAPD and SSR banding variation were similar (Figs. 1 and 2; comparative analysis not presented). The discriminatory power of both SSR and RAPD markers allowed for clear partitioning of Chinese × U.S. F_1 hybrids into broad groups related by pedigree and morphology (Figs. 2 and 3). Results indicate that polymorphic SSR and RAPD markers used herein may have utility for more extensive genetic analyses (e.g., mapping).

Genetic distance relationships

Estimates of GD could, if associated with combining ability, increase breeding effectiveness where wide crossing could lead to improved hybrid germplasm (i.e., heterotic effects). Moreover, if GD estimates

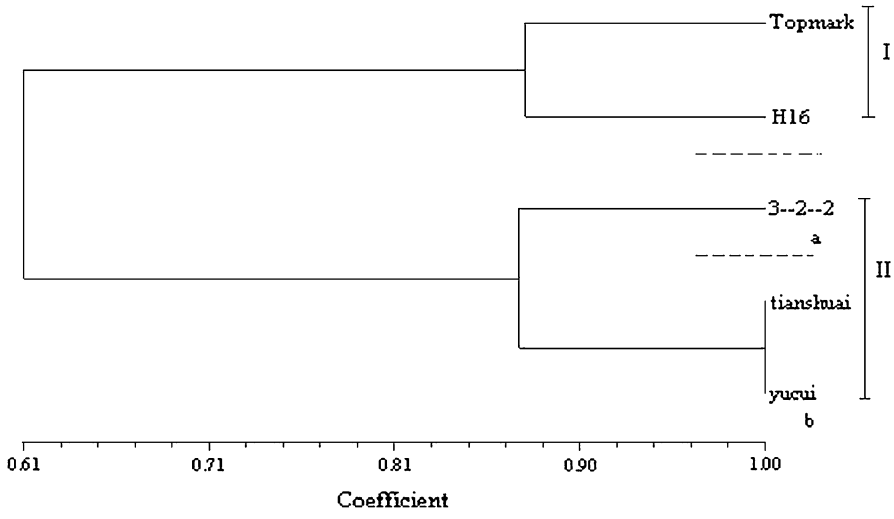

Fig. 1 Cluster analysis of melon (*Cucumis melo* L.) parental lines as grouped by 44 RAPD banding morphotypes

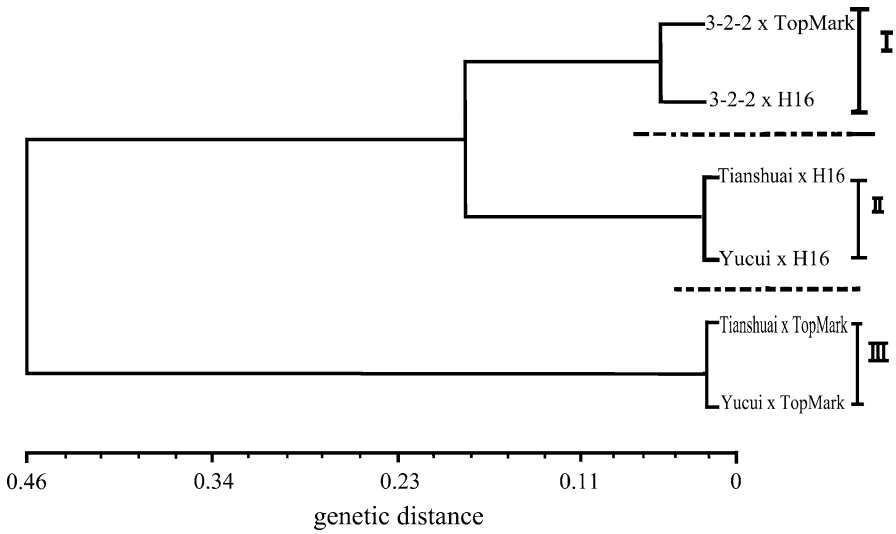

Fig. 2 Cluster analysis of melon (*Cucumis melo* L.) F_1 progeny as grouped by 39 SSR banding morphotypes

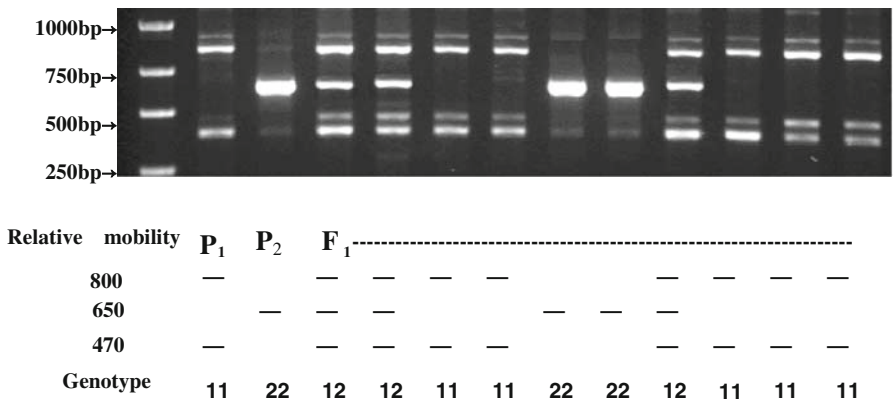

Fig. 3 Amplifications after electrophoresis of melon (*C. melo* L.) parental lines (lanes 2 and 3) and their derived F_1 cross-progeny (lanes 4-13) as primed using the RAPD C05 (lane 1 = 100 bp ladder)

could be shown to have predictive value (e.g., SCA relates to GD as a function of heterosis) leading to the successful introgression of economically important genes from exotic sources, then population development strategies could be improved to exploit potential heterotic groups. Examination of variation at RAPD and SSR loci indicted that there was considerable GD among parental lines (e.g., Chinese vs. U.S.; Fig. 1). Indeed, 'Top Mark' typifies the breath of genetic variation in Group *Cantalupensis* market types (Staub et al. 2000), where plants produce netted, orange flesh, sweet, climacteric fruit that abscise at maturity. With the exception of dominant vein tracts or sutures, line H-16 is also considered a Group *Cantalupensis* type with typical U.S. Western Shipping type fruit characteristics. Fruit of TM and line H-16 possess an orange mesocarp, and are relatively sweet [total soluble solids (TSS) = 9–10% BRIX] (unpublished data). In contrast, fruit of early flowering, non-netted, parental Chinese lines [TM (25 days) vs. line 3-2-2 (15 days) post-transplant] possess a white or green mesocarp (i.e., line 3-2-2 white), and may have variable TSS [5 (Wisc., U.S.A) to 15 (Harbin, China) % BRIX] depending on growing environment (unpublished data).

The average GD values among the five parental lines used herein were comparatively broad depending on the markers system employed (RAPD = 0.24 ± 0.15 vs. SSR = 0.53 ± 0.08) (data not presented). Nevertheless, RAPD-based and SSR-based cluster analyses revealed two similar parental relationship groupings (partial data presented), where, predictably, 'Top Mark' and line H-16 formed one group (Group 1) and Chinese lines (3-2-2, 'Tianshuai' and 'Yucui')

Table 3 Genetic distance (GD) estimates among F_1 melon (*Cucumis melo* L.) hybrids as defined by RAPD (Jaccard's GD; lower diagonal) and SSR (Nei's GD; upper diagonal) marker variation

RAPD[a]	SSR[b]					
	3-2-2 × TopMark	Tianshuai × TopMark	Yucui × TopMark	3-2-2 × H-16	Tianshuai × H-16	Yucui × H-16
3-2-2 × TopMark	0	0.11	0.11	0.05	0.05	0.05
Tianshuai × TopMark	0.46	0	0.05	0.15	0.05	0.15
Yucui × TopMark	0.46	0.0	0	0.10	0.15	0.10
3-2-2 × H-16	0.07	0.42	0.58	0	0.10	0.05
Tianshuai × H-16	0.13	0.37	0.63	0.63	0	0.05
Yucui × H-16	0.13	0.37	0.63	0.63	0.0	0

[a] Estimated according to Jaccard (1908)

[b] Estimated according to Nei (1973)

were partitioned into a second clade (Group 2) (Figs. 1 and 2). The Chinese lines (the second clade) could be further partitioned into two sub-groups, where line 3-2-2 formed sub-group one, and 'Yucui' and 'Tianshuai' (most related by pedigree) constituted sub-group two. These groupings are consistent with geographic origin [GD = 0.12–0.39 (RAPD) and 0.45–0.71 (SSR)] and market class differences [GD for 'Top Mark' vs. H-16 = 0.12 (RAPD) and 0.50 (SSR) markers and GD for 'Yucui' vs. H-16 = 0.39 (RAPD) and 0.71 (SSR)] (Tables 2 and 3). The average GD among parents as assessed by SSR markers analysis was larger than by RAPD marker analysis (Tables 2 and 3). This difference could be partly explained by marker type (dominant vs. codominant) and the magnitude of RAPD band variability typical of melon (López-Sesé et al. 2002, 2003). Nevertheless, these results indicate that genetically-based market type and geographical differentiation exist among parental lines employed.

Parental and hybrid marker-based comparisons can provide insights into GD predictability of genetic relationships. Hybrids were classified into three groups herein, where Group 1 consisted of 3-2-2 × 'Top Mark' and 3-2-2 × H-16, Group 2 contained Tianshuai × H-16 and Yucui × H-16, and Group 3 included Tianshuai × 'Top Mark' and Yucui × 'Top Mark' (Fig. 2). The average and range of GD estimates among hybrids varied with marker type [mean 0.09, range from 0.05 to 0.11(RAPD), and mean 0.39, range from 0.07 to 0.63 (SSR); Tables 2 and 3]. As might have been predicted from parental relationships, GD between hybrids 3-2-2 × H-16 and 3-2-2 × 'Top Mark' were relatively small [(GD = 0.07 (SSR); GD = 0.05 (RAPD)] when compared to hybrids 3-2-2 × H-16 and 'Tianshuai' × H-16 [GD = 0.63 (SSR); GD = 0.1 (RAPD)]. Likewise, hybrids 'Tianshuai' × 'Top Mark' and 'Yucui' × 'Top Mark' were distantly related [GD = 0.11 (SSR); GD = 0.46 (RAPD)]. Consistency in hybrid groupings by common parent, confirms maker predictability in the germplasm examined, and is suggestive of their potential utility for more broad-based germplasm comparisons.

Analysis of variance

The main effects of genotype and location, and genotype × locations interactions using combined trait data are given in Table 2. Analysis of variance revealed significant differences ($P \leq 0.05$, $P \leq 0.01$) for the traits examined, except for location effects on fruit and branch number, and on fruit L:D ratio, and the genotype x location interactions detected. Variance component analyses indicated that lateral branch and fruits/plant number differed among genotypes ($P \leq 0.05$). Location effects were significant for days to 50% female flower ($P \leq 0.01$) and fruits/plant ($P \leq 0.05$). Variance component analyses (i.e., likelihood ratio test) detected significant ($P \leq 0.05$, $P \leq 0.01$) genotype x location differences for all traits examined, except days to 50% female flower. Furthermore, significant ($P \leq 0.01$) genotype × location (G×L) interactions were detected for fruit number/plant and L:D ratio. These G×L interactions and those

Table 4 Mean squares (MS) with associated F-test values for traits in melon (*Cucumis melo* L.) partitioned by genotype (12) and location (3), and their interaction

Source of variance	df[b]	LBN[c]		DTF[d]		FN[e]		Yield[f]		df	Fruit L:D[g]	
		MS[h]	F	MS	F	MS	F	MS	F		MS	F
Genotype (G)	11	2.10	2.94*[i]	743.8	911.05**	104.81	14.94**	3.33	0.818*	11	0.021	0.49
Location[a] (L)	2	0.18	0.24	6.69	7.96**	2.42	0.34	3.58	0.86*	1	0.006	0.15
G×L	4	0.80	1.71*	0.88	0.18	7.41	4.29*	4.28	13.48**	2	0.021	2.19*

[a] Locations are open-field (USA), and energy-saving (PRC) and plastic greenhouses (PRC)

[b] *df* degree of freedom

[c] *LBN* lateral branch number from the first-true leaf node (no predominant main stem)

[d] *DTF* days to 50% flower from transplanting

[e] *FN* fruit number/plant; cumulative average over three harvests

[f] Average per harvest over three harvests

[g] *L:D* average fruit length/diameter ratio over three harvests

[h] *MS* mean squares

[i] *,** indicates that the effect is significant at the 0.05 and 0.01 probability level, respectively

Table 5 Phenotype correlations between morphological characteristics among parental lines and F_1 hybrids in melon (*Cucumis melo* L.) as examined in three growing environments

Traits	LBN[a]	DTF[b]	FN[c]	Yield[d]	Fruit L:D[e]
Energy-saving greenhouse (China)					
LBN		−0.4196	0.8427**	−0.4576	0.0145
DTF	−0.4196		−0.4278	0.2024	0.9620**
FN	0.8427**[f]	−0.4278		−0.7096	0.1175
Yield	−0.4576	0.2024	−0.7096		−0.0971
Fruit L:D	0.0145	0.9620**	0.1175	−0.0971	
Plastic greenhouse (China)					
LBN		0.1406	0.6384*	0.0857	−0.2296
DTF	0.1406		−0.0301	0.5479	−0.002
FN	0.6384*	−0.0301		−0.4275	−0.5963
Yield	0.0857	0.5479	−0.4275		0.8478**
Fruit L:D	−0.2296	−0.002	−0.5963	0.8478**	
Open-field (USA)					
LBN		−0.4196	0.7805**	−0.5234	
DTF	−0.4196		−0.3012	0.2545	
FN	0.7805**	−0.3012		−0.7555	
Yield	−0.5234	0.2545	−0.7555		

[a] LBN = lateral branch number from the first-true leaf node (no predominant main stem)

[b] *DTF* days to 50% flower from transplanting

[c] *FN* fruit number per plant; cumulative average over three harvests

[d] Average per harvest over three harvests

[e] *L:D* average fruit length/diameter ratio over three harvests

[f] *,** indicates that the effect is significant at the 0.05 and 0.01 probability level, respectively

detected for fruit and branch number per plant (Table 4; ($P \leq 0.05$)) were, in part, likely due to soil differences characteristic of the diverse growing environments employed for evaluation. These results indicated that breeding for high yield cultivars will require multiple location testing.

Trait variation and correlation

There were large and significant ($P \leq 0.05$) environmental effects for all traits examined, except fruit size (L:D) (Table 5). Such effects were predictable given the dramatic differences in growing environments (i.e., ESG vs. PG vs. OF). Generally, the number of fruit harvested in the ESG was higher than in the PG and OF growing environments. However, fruit L:D values were generally similar in all locations.

Initial phenotypic performance analyses within locations revealed the presence of significant variation among F_1 progenies across locations for all traits examined where performance was location dependent (Table 5). For instance, 'Top Mark' produced the highest number of lateral branches in OF and PG, but its derived progeny developed comparatively few lateral branches in these growing environments. Similarly, average fruit weight was highest and days to 50% flower were greatest in the OF when compared to the other test environments. In contrast, lateral branch number and fruit number per plant were highest in the ESG. Moreover, hybrid progeny derived from line H-16 mating tended to produce more fruit per plant when compared to other hybrid progeny, but lateral branch number, days to 50% flower and fruit number were similar in the three growing locations. Thus, morphological differences in hybrid progeny depended upon both parental genotype and environment.

Correlation values between traits were moderately high ($r > 0.4$) in all locations (data not presented). For instance, fruit weight and number were positively correlated ($r > 0.80$) in the ESG. Likewise, correlation values were relatively high (0.94) between days to 50% flower and branch number in ESG. Similarly, correlation values between fruit number and fruit weight were high depending on the growing environment [$r = 0.90$ (ESG), 0.70 (PG), and 0.90 (OF)]. In contrast, correlation values between L:D in PG ($r = 0.01$) and ESG ($r = 0.12$) growing environments were not high when compared to OF ($r = 0.46$) growing conditions. Results indicate that, although several factors influence vegetative development, effects can be growing environment specific. Beavis et al. (1994), in fact, demonstrated that the action of yield-associated quantitative trait loci (QTL) in maize progeny (Topcross and F_4) differed across OF growing environments. In that case, interpretation of QTL by environment interactions allowed for characterization of environmentally dependent QTL effects on seed number and weight. Thus, the characterization of the hybrid performance and environment interactions (i.e., combining ability and heterosis) described herein (Tables 5 and 6) is critical for the development of melon breeding strategies that optimize economically important gene action and interactions in the populations examined.

Combining ability

Environment can have a dramatic effect on plant performance in cucurbit crop species (e.g., plant density; Wehner 2002). In our study, parental lines and often hybrid performance was environmentally dependent (e.g., days to flower and lateral branch number. The observed GCA × location interaction effects for days to flower and lateral branch number were primarily a function of changes in relative magnitude and not rank between different locations.

Combining ability effects were often inconsistent over locations, and thus are presented by location. General combining ability estimates were, however, commonly positive in ESG and PG growing environments. The general significance of GCA and SCA effects suggests that genetic differences exist among parental lines. For instance, when 'Top Mark' was used as the paternal parent, derived hybrid progeny performed typically better for various traits than F_1 progeny derived from its closely related counterpart, line H-16. Moreover, in certain instances, hybrid performance differences were associated with the degree of genetic affinity (i.e., GD) between the parental lines.

Fruit number and weight

While positive SCA directional effects were detected for fruit weight in 'Tianshuai' × 'Yucui' progeny in all locations, consistent negative SCA directional

Table 6 Estimates of general (GCA) and specific (SCA) combining ability for morphological traits in melon (*Cucumis melo* L.) as defined in three growing locations

	Energy saving greenhouse[b]			Plastic greenhouse[c]			Open-field[d]		
	MS	F	R^2 [k]	MS	F	R^2	MS	F	R^2
GCA[a]									
LBN[e]	2.95	10.03** [j]	0.80	16.02	58.18**	0.96	0.13	1.59	0.39
DTF[f]	2.38	1.74*	0.41	1.129	5.54**	0.69	0.63	1.22	0.33
Yield[g]	0.45	522.43**	0.98	1.25	51.3**	0.95	21.43	3.04*	0.55
FN[h]	0.13	239.9**	0.98	0.75	8.14**	0.76	3.81	12.94**	0.84
Fruit L:D[i]	0.002	0.33	0.12	0.002	0.02	0.01			
SCA									
LBN	2.14	4.68**	0.66	2.54	3.09*	0.562	0.098	0.25	0.09
DTF	0.02	0.02	0.01	3.28	44.39**	0.94	0.82	0.69	0.22
Yield	0.88	411.16**	0.99	0.07	6.40**	0.72	111.2	13.35**	0.84
FN	0.32	139.56**	0.98	0.26	4.8**	0.66	10.06	2.77*	0.53
Fruit L:D	0.001	0.99	0.29	0.004	0.36	0.13			

[a] General combining ability

[b] Plastic active solar heating, PCR

[c] Plastic, solar heating, PRC

[d] Open field, USA

[e] *LBN* lateral branch number from the first-true leaf node (no predominant main stem)

[f] *DTF* days to 50% flower from transplanting

[g] Average per harvest over three harvests

[h] *FN* fruit number/plant; cumulative average over three harvests

[i] *L:D* average fruit length/diameter ratio over three harvests

[j] *,** indicates that the effect is significant at the 0.05 and 0.01 probability level, respectively

[k] *MS* Mean square, *F* Freedom, R^2 coefficient of determination

effects were identified in 'Tianshuai' × H-16 progeny. Significant trait differences ($P = 0.05$) between the parents of these crosses were also detected across locations. In the main, hybrid plant performance for the traits examined was directly related to the influence of parental lines as estimated by combining ability.

Fruit shape

Even though estimates of GCA were highest for 'Top Mark' in all locations, GCAs associated with line H-16 hybrid performance were comparatively low (Table 5). Curiously, significant positive SCA directional effects were identified for those crosses involving line H-16, but negative SCA direction effects were detected for a majority of the crosses involving 'Top Mark'. Mean performance differences between parent lines for fruit shape in PG environments was, however, not significant (OF not evaluated) (Table 7).

Branch number and days to 50% flower

The highest positive GCA values for days to flower of the hybrids tested were derived from crosses involving 'Tianshuai'. Positive GCA values for days to 50% flower were associated with the parental 'Top Mark', and negative GCA effects for this trait were associated with its closely related counterpart, line H-16. In contrast, performance (GCA values) of progeny derived from the highly branched line 3-2-2 (Chinese) indicated that this line did not contribute significant genetic factors for multiple lateral branching and reduced days to anthesis to its progeny. Likewise, despite its potential for contributing multiple branching to its progeny, the SCA effects

Table 7 Means by location of morphological traits in melon (*Cucumis melo* L.) parental lines

Parent	LBN[a]	DTF[b]	FN[c]	Yield[e]	Fruit L:D[f]
Energy-saving greenhouse (ESG)[d]					
Female					
Tianshuai	5.67a	25b	4.0ab	1.31a	1.10b
Yucui	6.43a	28a	4.9a	1.70a	1.10b
Line 3-2-2	4.20b	29a	2.8b	2.53a	1.53a
Male					
TopMark	4.17a	28.3a	1.67b	1.64a	1.33a
Line H-16	4.06a	26.7a	3.63a	1.17a	1.33a
Grand mean	4.906	27.4	3.4	1.67	1.278
Plastic greenhouse (PG)					
Female					
Tianshuai	19.3a	5.7a	3.8a	0.883b	1.1b
Yucui	18a	4.9a	4.2b	0.964b	1.1b
Line 3-2-2	17.7a	4.3a	2.3b	1.496a	1.496a
Male					
TopMark	24a	4.7a	2.2b	1.54a	1.33a
Line H-16	19b	4.3a	3.6a	0.72b	1.33a
Grand mean	19.6	4.78	3.22	1.72	1.27
Open-filed in USA (OP)					
Female					
Tianshuai	3.93a	18.7a	4.83a	1.49b	–
Yucui	3.96a	19.3a	4.73a	1.59b	–
Line 3-2-2	4.03a	20.7a	2.63b	4.78a	–
Male					
TopMark	4.67a	27.7a	3.16a	2.09a	–
Line H-16	3.86a	19.7b	1.86a	3.76a	–
Grand mean	4.09	21.22	3.442	2.743	–

[a] *LBN* lateral branch number from the first-true leaf node (no predominant main stem)

[b] *DTF* days to 50% flower from transplanting

[c] *FN* fruit number/plant; cumulative average over three harvests

[d] Plastic, active solar heating

[e] Average per harvest over three harvests

[f] *L:D* average fruit length/diameter ratio over three harvests

associated with branch number in 'Tianshuai' were comparatively low and negative.

The significance of GCA for branch number effects (Table 6) indicated that dominance and/or epistasis contributed to the observed genetic variation. However, the general lack of significant for male × female interactions when compared to the highly significant male and female effects suggests that most of genetic variation in branch number in this study was due to additive genetic effects. In fact, when taken collectively, our results parallel those of Kupper and Staub 1988 who assessed similar traits in exotic, highly branched cucumber hybrids [*C. sativus* var. *sativus* × *C. sativus* var. *hardwickii* (R.) Alef.]. They reported that both GCA and SCA were significant for most of the yield-related characters evaluated in the lines tested, and that the magnitude of the contribution of SCA was generally less than GCA, suggesting that additive effects were more important than non-additive effects. In Kupper and Staub 1988 and our study, location effects were important in trait expression (magnitude and direction of GCA and SCA effects), and significant differences in hybrid performance were based on the parental contributions.

Estimates of the average performance of a line in hybrid combination were provided herein by GCA (Table 6). Additive and dominance effects have been shown to influence trait expression for fruit number and later branch number in cucumber (Kupper and Staub 1988). The GCA of line 3-2-2, 'Tianshuai' and 'Yucui' were different based on their performance when used in hybrid combination with 'TopMark' and line H-16. Although line 3-2-2 and 'Tianshuai' conditioned an increase in fruit weight, L: D ratio and branch number, 'Yucui' decreased flower days in hybrid progeny.

The SCA effect varied between the ESG and PG which was not surprising since environmental effects were large with regards to the expression of yield components (e.g., days of first flower, fruit number) (Table 6). Both GCA and SCA effects were significant determinants of the yield- related traits studied. Theoretically, GCA analysis can be valuable for predicting hybrid performance in melon breeding. Similarly, the coefficient of determination (R^2) can provide an estimate of hybrids performance based on per values of parents, and permits comparison with other predictors based on GCA. Such comparisons and contrasts will allow unique lines such as 3-2-2 and H-16 to be used effectively in plant improvement (i.e., population development).

Heterosis and relative genetic distance

The genetic basis of heterosis has been the subject of much debate. Nevertheless, heterosis has been effectively employed to increase hybrid performance in

Table 8 The relationship between GD and heterosis in melon (*Cucumis melo* L.) defined by yield component traits examined in three growing locations

Traits	LBN[a]	DTF[b]	FN[c]	Yield[d]	Fruit L:D[e]
Energy-saving greenhouse (China)					
MH	0.5328	0.3155	−0.9716	0.5216	0.6358
HH	−0.2249	0.1559	−0.9979	0.6176	0.5510
RHH	−0.3650	03407	−0.9749	−0.6103	−0.4557
Plastic greenhouse (China)					
MH	0.7605	0.100	−0.0401	−0.0849	0.5390
HH	0.6145	0.0831	−0.2951	0.3060	0.2975
RHH	0.6397	−0.1553	0.2815	−0.5417	−0.1696
Open-field (USA)					
MH	0.8513**[f]	0.4743	0.6433	−0.1074	
HH	0.8931*	0.6070	0.6377	−0.2049	
RHH	−0.8935	−0.0608	0.7848	−0.0611	

[a] *LBN* lateral branch number from the first-true leaf node (no predominant main stem)

[b] *DTF* days to 50% flower from transplanting

[c] *FN* fruit number/plant; cumulative average over three harvests

[d] Average per harvest over three harvests

[e] *L:D* average fruit length/diameter ratio over three harvests

[f] *,** indicates that the effect is significant at the 0.05 and 0.01 probability level, respectively

many crop species. For instance, "Piel de Sapo" × exotic (*C. melo* subsp. *agrestis*) hybrids demonstrated heterosis (<80%) for fruit quality (average parental heterosis = −5.46%; Monforte et al. 2005). In contrast, hybrid heterotic effects for the yield components examined in progeny derived from closely related parents examined herein (e.g., 'Tianshuai' and 'Yucui') were not detected herein. Where heterosis was detected, it was associated with growing conditions (e.g., larger heterotic effects associated with ESG cultivation than in other locations) for the traits examined (data not presented). The greatest high-parent heterosis (PH = 692.9%) and mid-parent heterosis (MP = 535.3%) was detected for weight per melon in line 3-2-2 × H-16 (ESG) and 'Yucui' × 'TopMark' (PG) progeny, respectively (Table 8). In contrast, the average of relative high-parent heterosis (RHH = 518.2%) was detected in line '3-2-2' × 'Top Mark' progeny grown in the OF for weight per melon. The effective use of heterosis in plant improvement programs requires sufficiently large and predictable heterotic effects, especially where progeny performance is environmentally dependent. Given that estimated mid- and high-parent heterosis are high in Chinese-derived hybrids and growing environment effects (ESG and PG) have been characterized in the populations examined, breeding strategies can now be developed which optimize potential heterotic effects in these economically important Chinese breeding lines as applied to the environments evaluated.

Prediction of hybrid performance based on the relationship between genetic relatedness and heterosis in crop species is unclear and likely species dependent (Singh and Sharma 1989; Teklewold and Becker 2006). Some data indicate that correlative values between these genetic estimates can be used to predict hybrid performance (Ali et al. 1995; Xiao et al. 1996), while others indicate that such correlations have limited value (Cheres et al. 2000) or no value (Chowdran et al. 1998). Therefore, the association between GD and heterosis was investigated to determine if melon lines derived from exotic sources (landraces) could be chosen for hybrid production based on their relatedness. Phenotypic correlations between GD and heterosis varied dramatically across growing environments [i.e., OF (r from −0.89 to 0.85), ESG (r from −0.97 to 0.76), and PG (r from

−0.29 to 0.76)] depending on the trait examined (Table 8). Likewise, the relationship between mid-parent-heterosis (MH) and GD and between high-heterosis (HH) and GD for branch number in the open-field was significant ($r = 0.85$ and $r = 0.89$, respectively) ($P \leq 0.05$), other GD and heterotic relationships between traits were not.

In the main, however, consistent correlations could not be detected and positive correlations between GD and heterosis was largely cross specific. In crosses where such positive correlations were detected, additional conformational experiments must be conducted before their potential predictive value can be used in melon breeding. Although the RAPD and SSR marker genotyping described herein offered a reliable and effective way of assessing genetic variation, hybrid heterosis could not be accurately predicted from parental genetic distances. Nevertheless, crossing between market classes of diverse origin would be warranted when program objectives are to increase genetic diversity and/or introgress specific economically important traits in melon (e.g., crisp texture of Group Inodorous/Conomon Chinese melon into Group Cantaloupensis U.S. Western Shipping types).

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